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Development of Temporal and Spatial Bimanual Coordination During Childhood

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Developmental changes in bimanual coordination were examined in four age groups: 6/7, 10/11, 14/15 years, and young adults. Temporal coupling was assessed through the stabilizing contributions of interlimb interactions related to planning, error correction, and reflexes during rhythmic wrist movements, by comparing various unimanual and bimanual tasks involving passive and active movements. Spatial coupling was assessed via bimanual line-circle drawing. With increasing age, temporal stability improved. Relative contributions of planning and reflex interactions to the achieved stability did not change, whereas error correction improved. In-phase and antiphase coordination developed at similar rates; implications of this result were discussed in terms of mirror-activity inhibition. Overall spatial drawing performance (circularity, variability, smoothness) improved with age, and spatial interference was smaller in adults than children. Whereas temporal coupling increased from 6/7 years to adulthood, spatial coupling changed mainly after 14/15 years. This difference in the development of temporal and spatial coupling corresponds to the anterior-posterior direction of corpus callosum myelination as reported in the literature.

Keywords: motor development, bimanual coordination, interlimb interactions, rhythmic coordination, spatial coordination

Bimanual coordination is required in many daily life activities, such as cooking, writing, and getting dressed. To successfully coordinate bimanual movements, information needs to be exchanged between the cerebral hemispheres. The primary structure for interhemispheric communication is the corpus callosum (CC), which allows interhemispheric integration of motor, sensory, and cognitive processes (Muetzel et al., 2008; Wolff, Kotwica, & Obregon, 1998). The myelin sheath around the CC fibers enables rapid and synchronized information transfer. During development across childhood this myelin sheath matures, increasing the rate of interhemispheric communication (Deoni et al., 2011; Giedd et al., 2009). To examine the effects of these developmental changes on bimanual coordination, we examined bimanually coordinated movements across different age groups. Although developmental changes in other brain structures and networks may contribute to improved motor control and bimanual coordination as well, our predictions regarding the

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changes in interlimb coordination were based on pertinent literature regarding CC functioning in relation to bimanual temporal and spatial coordination.

1.1 Corpus Callosum

Myelination of the CC not only leads to rapid and synchronized information transfer, but it may also enhance interhemispheric inhibition of mirror movements (Daffertshofer, Peper, & Beek, 2005; Hubers, Orekhov, & Ziemann, 2008). Mirror movements—unintended movements of the limb that is not active during intended unilateral movements of the contralateral limb—are often observed in young children. Communication via the CC may result in mirror activity (e.g., interference effects disappear in callosotomy patients, see below), but mirror movements are also suppressed via interhemispheric inhibition across the CC (Hubers et al., 2008; Mayston, Harrison, & Stephens, 1999). During development the occurrence of mirror movements decreases in frequency and intensity; around the age of 10 a sharp decline has been observed, possibly as a result of CC myelination (Cincotta & Ziemann, 2008; Cohen, Taft, Mahadeviah, & Birch, 1967; Hubers et al., 2008). Since in everyday tasks the two hands often have to execute different movements simultaneously, increased mirror movement inhibition with age will lead to improved bimanual coordination and hence improved task execution.

Studies with callosotomy patients—i.e., patients in whom (part of) the CC has been dissected—have highlighted the importance of the CC in bimanual coordination. These patients made fewer errors than control participants in spatially incompatible drawing tasks, indicating that the tendency to execute the same movements during bimanual coordination was suppressed as a result of their callosotomy. In other words, spatial coupling of the hands appears to be organized via the CC (Eliassen, Baynes, & Gazzaniga, 2000; Franz, 1997; Franz, Eliassen, Ivry, & Gazzaniga, 1996), particularly via its posterior part (Eliassen, Baynes, & Gazzaniga, 1999). The anterior part of the CC has been shown to be involved in temporal coupling (Eliassen et al., 1999; Ouimet et al., 2010), albeit in a task-dependent manner (Ivry & Hazeltine, 1999; Kennerley, Diedrichsen, Hazeltine, Semjen, & Ivry, 2002; Tuller & Kelso, 1989). Specific parts of the CC thus appear to be involved in different coupling processes in bimanual coordination: the posterior part primarily in spatial coupling and the anterior part primarily in temporal coupling.

Based on in vitro studies, it has been suggested that CC myelination during development is completed around the age of 10 or 11 (cf., see discussion in Fagard, Morioka, & Wolff, 1985). However, more recent magnetic resonance imaging (MRI) studies revealed that myelination is not completed until the early twenties (Giedd et al., 1996; Rajapakse et al., 1996; Thompson et al., 2000). In a longitudinal study, Thompson et al. (2000) showed that specific parts of the CC differ in growth rates: the anterior parts grow fastest between the age of 3–6, while the largest posterior growth was observed between the age of 6–15. Because callosotomy studies indicated that these parts of the CC are differentially involved in the spatial and temporal aspects of bimanual coordination, the question arises how these aspects of bimanual coordination are mediated by CC myelination during childhood. In this study we therefore examined how temporal and spatial coupling of the limbs change across childhood.

1.2 Temporal Bimanual Coupling

Temporal coupling between the limbs has been investigated in a variety of tasks and across various ages. Performance has been found to improve with age in children in bimanual tapping (Muetzel et al., 2008; Wolff et al., 1998), bimanual circle drawing (Robertson, 2001), bimanual reaction tasks (Fagard, Hardy-Leger, Kervella, & Marks, 2001), and clapping (Fitzpatrick, Schmidt, & Lockman, 1996). CC myelination was demonstrated to contribute positively to alternate tapping performance (Muetzel et al., 2008).

A task that is often used to examine temporal interlimb coupling is isofrequency bimanual coordination, usually by studying the relative phase between the hands (Φ) and its variability (Haken, Kelso, & Bunz, 1985; Kelso, 1984; Schöner, Haken, & Kelso, 1986). As a result of interlimb interactions, only two coordination patterns can usually be executed stably without learning: in-phase (IP) and antiphase (AP) coordination (Zanone & Kelso, 1992). IP coordination ($\Phi = 0°$) refers to mirror-symmetric movements or the simultaneous activation of homologous muscles, whereas AP coordination ($\Phi = 180°$) refers to parallel movements or the simultaneous activation of nonhomologous muscles. AP is less stable than IP coordination, and when frequency increases to a critical value, an involuntary switch from AP to IP may occur (Haken et al., 1985; Schöner et al., 1986). The coupling between the limbs and these differences between IP and AP coordination are the result of interlimb interactions. When studying bimanual coordination across different age groups, the question arises how these interactions contribute to developmental changes in bimanual coordination. But what are these interlimb interactions and how may they evolve during development?

Recently, specific forms of interlimb interaction that underlie the stability of coordination patterns have been investigated in relation to the coordination pattern performed (Ridderikhoff, Peper & Beek, 2005), movement frequency (de Boer, Peper, & Beek, 2011), and the associated attentional costs (Ridderikhoff, Peper, & Beek, 2008). In particular, three forms of interlimb interactions can be dissociated based on the dependence on afferent, sensory information and the intention to execute a specific pattern (see Table 1). First, *movement planning* reflects interaction processes related to feedforward timing of the efferent signals that specify

Table 1 Sources of Interlimb Interaction Underlying Bimanual Coordination.

Interlimb interaction		Afference dependence	Bimanual intentionality
Planning	Generation of an integrated control signal for both limbs, specifying the bimanual pattern	No	Yes
Correction	Correction of relative phase errors based on kinesthetic afference, stabilizing the bimanual pattern	Yes	Yes
Reflex	Phase entrainment by contralateral afference	Yes	No

the bimanual coordination pattern, without taking adjustments based on afferent feedback into account. Second, *error correction* pertains to the correction of perceived relative phasing errors based on kinesthetic afference, to stabilize the intended bimanual coordination pattern. Third, *reflex interactions* refer to the unintentional attraction to specific phase relations between the limbs. This is a relatively automatic or reflex-like mechanism based on kinesthetic signals. Whereas error correction concerns the intentional use of kinesthetic feedback to correct for relative phase errors in the intended pattern, reflex interactions result in unintended attraction toward IP or AP coordination with the movements of the contralateral limb (Ridderikhoff, Peper, & Beek, 2006; Serrien, Li, Steyvers, Debaere, & Swinnen, 2001).

Planning, correction, and reflex interactions can be assessed by comparing specific tasks in which the interactions are present to a different extent, as demonstrated by Ridderikhoff, Peper et al. (2005). As we were testing children in the current study, we used a limited number of tasks and conditions (see Ridderikhoff et al., 2008, for a detailed description). All four tasks involved unimanual or bimanual rhythmic flexion-extension movements about the wrist. The tasks differed with regard to the degree in which the three sources of interaction are assumed to be involved (cf. Table 2): (1) in task UN (unimanual coordination with the metronome) no interlimb interactions are present; (2) in task UNm (task UN while a motor moves the contralateral hand) reflex interactions entrain the active hand to the passively moving hand; (3) in task KT (kinesthetic tracking) correction interactions furthermore stabilize the coordination pattern based on kinesthetic signals; (4) in task AB (active bimanual coordination) planning interactions further stabilize the coordination pattern. Systematic pairwise comparisons of two tasks can be used to single out the contributions of each of the sources of interlimb interaction (cf. Table 2): reflex interactions can be studied by comparing UNm and UN, correction interactions by comparing KT and UNm, and planning interactions by comparing AB and KT. Previous results showed that this method yields a useful dissociation between the contributions of the interlimb interactions in question to the stability of bimanual coordination, but that the sources do not add up linearly (as suggested

Table 2 Tasks and Sources of Interlimb Interaction.

Task		Planning	Correction	Reflex
AB	Active bimanual coordination at a tempo specified by an auditory signal.	X	X	X
KT	Kinesthetic tracking of the passively moving contralateral hand.		X	X
UNm	Unimanual coordination with an auditory pacing signal while (phase-shifted) passive movements of the contraleral hand are presented as distractor.			X
UN	Unimanual coordination with an auditory pacing signal.			

Mapping of the four tasks to the three sources of interlimb interaction. The "X" symbols represent the sources of interlimb interaction that are assumed to be involved in the associated tasks.

in Table 2). In particular, error correction appeared to be hardly involved in AB, because the planning interactions provided sufficient stability. Therefore, planning interactions were also examined by comparing AB to UNm (de Boer et al., 2011; Ridderikhoff, Peper et al., 2005).

1.3 Spatial Bimanual Coupling

The effects of development across childhood on spatial coupling in bimanual coordination have seldom been studied. Spatial coupling between two hands can be assessed in bimanual incompatible drawing (i.e., incompatible orientations or shapes), to determine how the hands affect each other. Spatial incompatible drawing has only been examined in adults (Eliassen et al., 1999; Franz et al., 1996; Franz, Zelaznik, & McCabe, 1991; Swinnen, Dounskaia, Levin, & Duysens, 2001) and in children with a disorder (Volman, 2005). Bimanual drawing has been studied across age groups (Lantero & Ringenbach, 2007; Robertson, 2001), but these studies did not involve incompatible drawing.

In the present experiment, we therefore assessed the developmental effects on spatial coupling by asking various age groups to draw two different shapes simultaneously. We used line-circle drawing, as this task is also feasible to perform by young children (Volman, 2005). For these line-circle drawings, unimanual drawings and bimanual drawings of the same shape served as control conditions. In this way, the development of spatial drawing of two different shapes (i.e., bimanual line-circle drawing) was contrasted to changes with age in unimanual drawing with the left and right hand (i.e., unimanual line and unimanual circle drawing) and to changes in bimanual drawing of the same shape (i.e., bimanual line-line and circle-circle drawing).

1.4 Aims and Hypotheses

The leading research question of the experiment was: How do spatial and temporal coupling of the hands develop across childhood? Children between 6–15 years of age were tested in the experiment. This age span was chosen in view of CC growth rates (Thompson et al., 2000) and the ability of young children to attend to the task and pace their movements with a metronome (Fitzpatrick et al., 1996). Notably, the tasks used in the present experiment were neither purely temporal nor purely spatial, as the “spatial” drawing tasks also involved timing of the hands and the “temporal” bimanual patterns involved spatial aspects like amplitude and direction. However, these tasks emphasized one particular aspect and were therefore used to examine either temporal or spatial coupling between the limbs.

With respect to the suggested anterior-posterior direction of myelination (Giedd et al., 1996; Thompson et al., 2000), the largest changes in temporal coupling were expected in the younger age groups compared with the older, whereas the opposite was expected for spatial coupling. Both IP and AP coordination were predicted to improve across development, but the largest improvements were expected to occur for AP, due to CC myelination and associated inhibition of mirror movements (Hubers et al., 2008; Mayston et al., 1999). This differential improvement of IP and AP was predicted for planning and correction interactions only, because these interlimb interactions are assumed to involve interhemispheric communication and both interactions contribute to the differential stability of IP and AP coordination (de Boer et al., 2011; Ridderikhoff, Peper et al., 2005). Potential age-related changes in reflex interactions were expected to be equally strong for IP and AP (Ridderikhoff, Peper, et al., 2006). Regarding spatial coupling, performance in the drawing task was expected to increase in all conditions because children typically become more skilled in drawing with age. In addition, due to CC myelination and associated inhibition of mirror activity, the attraction of each hand to the contralateral hand was expected to weaken with age. As a result, the distortions that were predicted to deteriorate performance when drawing two different shapes (relative to the control conditions) were expected to become smaller with age.

2. Method

2.1 Participants

Four age groups were examined: 6/7 years, 10/11 years, 14/15 years, and young adults (mean age 26.2 years, standard deviation (*SD*) 1.70 years). In each group 10 participants were tested (5 female, 5 male). All participants were right-handed as determined on a shortened version of the Edinburgh handedness scale (Oldfield, 1971; in view of the youngest age group two questions were removed: dealing cards and striking a match). Informed consent was provided before the experiment by the parents of the children and by the adults. Children received a small present after participating in the experiment.

2.2 Apparatus

To assess the temporal coupling between the hands and underlying interlimb interactions, a setup was used that has been described in detail elsewhere (Ridderikhoff, Peper et al., 2005). In short, participants sat in a height-adjustable chair with their elbows slightly flexed and their feet supported. Their forearms were placed on armrests in a neutral position (thumbs up, palms facing inward, fingers extended). Both hands were fixated to two flat manipulanda, allowing wrist flexion and extension only. The manipulandum for the left hand registered the wrist movements using a potentiometer, whereas that for the right hand either registered its movements (potentiometer) or controlled the wrist movements by means of a motor (i.e., for active and passive movements, respectively). A screen was used to eliminate visual feedback of the hand movements.

For spatial drawing, participants sat in a height-adjustable chair behind a table with a drawing tablet (Intuos A4 serial tablet, sample frequency 100 Hz, spatial accuracy 0.25 mm) on which they could make drawings with one or two cordless pens (Intuos standard pens). Templates that specified the shape(s) were placed on the tablet underneath a transparent cover. Participants were instructed to trace the presented shapes while looking at their hands. The vertically-oriented lines were 9 cm long and the circles had a diameter of 9 cm; line thickness of both shapes was 1.1 mm. The center-to-center distance between two shapes was 14.8 cm.

For both the temporal and spatial tasks, auditory pacing stimuli (pitch: 440 Hz, duration: 50 ms) were presented through speakers positioned close to the participant.

2.3 Procedure

The order of the temporal and spatial coordination parts was quasi-counterbalanced across participants (i.e., over each age-gender subgroup).

2.3.1 Temporal Coordination. Participants executed four different tasks that involved unimanual or bimanual rhythmic flexion-extension movements about the wrist. Starting with UN, participants performed unimanual rhythmic flexion-extension movements of their left wrist at the tempo specified by the auditory signal. Participants were instructed to let peak flexion coincide with the beep. Next, participants executed bimanual coordinated movements (task AB) of the wrist in IP or AP coordination. During IP peak flexion of both hands had to coincide with the beep, while for AP peak flexion of the left hand and peak extension of the right hand had to coincide with the beep.

In tasks UNm and KT the right hand was moved by the motor. The motor trajectories were based on sinusoidal trajectories, with an amplitude of 25° (peak-to-peak 50°) around a wrist position of 10° in flexion (i.e., approximately the neutral position). To prevent the trajectories from being perceived as predictable, the period lengths and the amplitudes of the cycles were randomly varied to obtain a moderate level of variability: $SD_{\text{frequency}} = 0.02$ Hz and $SD_{\text{amplitude}} = 3.6°$ (i.e., in accordance with Ridderikhoff, Peper, & Beek, 2007). In UNm, four phase relations between the passive movements and metronome pacing were applied: a phase shift of -30° and 0° around IP and AP (with 30° corresponding to 1/12th of a movement cycle and the negative phase shift implying a phase advance of the passive movements). The passive movements were phase shifted using cubic spline interpolation at the start of the trial so that the phase shift of -30° was achieved in three cycles. The trajectories were multiplied with a windowing function to generate a smooth increase and decrease in the amplitude of the passive movements in the first and last two cycles respectively. In task UNm, participants were instructed to ignore these passive movements and to let peak flexion of their active (left) hand coincide with the beep (i.e., as in task UN). In task KT participants were instructed to move their active hand so as to track their passively moving hand, either in IP or AP (again defined in terms of the phase relation at the turning points of the movements). In this task, no pacing signal was present.

Each condition was repeated twice. Thus, in total, 2 UN trials, 2 (Pattern) × 2 (Repetitions) = 4 AB trials, 2 (Pattern) × 2 (Shift) × 2 (Repetitions) = 8 UNm trials, and 2 (Pattern) × 2 (Repetitions) = 4 KT trials were executed. Trials were grouped in several blocks which were ordered according to instruction and difficulty: UN, AB-IP, AB-AP, UNm, KT-IP, and KT-AP. Before each block a single practice trial was presented. In all conditions frequency was set to 1.1 Hz and trial length was 21 cycles.

2.3.2 Spatial Coordination. Participants executed five conditions, which were ordered according to difficulty to facilitate their performance by the children: (1) Unimanual circle drawing with the right hand; (2) Unimanual line drawing with the left hand; (3) Bimanual-same, circle: bimanual circle drawing; (4) Bimanual-same, line: bimanual line drawing; and (5) Bimanual-different: drawing a line with the left hand and a circle with the right hand. Each condition was repeated twice. For circle drawing, movement direction was specified: the right hand drew the circles in counterclockwise direction and the left hand in clockwise direction (i.e., bimanual circle drawing was mirror symmetrical). Movement frequency was set to 1.0 Hz and trial duration was 20 s. A pacing signal prescribed movement frequency: participants were instructed to complete one circle and/or line (up and down) for each beep. Participants were free to choose which point of the line or circle to synchronize with the beep.

2.4 Data Analysis

2.4.1. Temporal Coordination The first and last three cycles of each trial were removed, leaving 15 cycles for analysis. More cycles were removed if (1) Φ increased or decreased progressively over several consecutive cycles (i.e., phase wrapping); (2) the phase relation with the pacing signal or between the hands was not correct (i.e., in case of a switch to the other pattern). The cycles included in the analysis were low-pass filtered (2nd-order bidirectional Butterworth filter, cut-off frequency 18 Hz). For the tasks in which two hands were involved (AB, KT, and UNm), the relative phase between the hands was calculated for each cycle as $\Phi_i = 360° (t_{y,i}—t_{x,i}) / (t_{x,i+1}—t_{x,i})$, where $t_{y,i}$ and $t_{x,i}$ indicate the time of the ith peak flexion (extension) of the left hand and the right hand, respectively (cf. Carson, Goodman, Kelso, & Elliott, 1995). For the unimanual tasks (UNm and UN), the relative phase between the metronome and peak flexion of the left hand was determined for each cycle as $\Psi_i = 360° (t_{y,i}—t_{x,i}) / (t_{x,i+1}—t_{x,i})$, where $t_{y,i}$ indicates the time of the ith peak flexion of the left hand and $t_{x,i}$ corresponds to the moment of the ith metronome beep. For both Φ and Ψ a positive value implied that the left hand (y) was lagging the reference signal (x). Circular statistics (Mardia, 1972) was used to determine the average values of Φ and Ψ, and the corresponding circular standard deviations (CSD_Φ and CSD_Ψ). To assess accuracy, the absolute error in Φ was calculated as $AE_\Phi = | \Phi — \Phi_{required} |$ with $\Phi_{required}$ equal to 0° and 180° for IP and AP, respectively.

An error in relative phasing can be corrected by shortening or lengthening the subsequent half cycle of (one of) the hands, resulting in a negative correlation between the signed error in relative phasing at peak flexion or extension and the duration of the subsequent half cycle (Ridderikhoff et al., 2007). Therefore, the presence of error correction was examined in terms of this error correction correlation (R_{EC}), calculated for each half cycle of the left hand (i.e., the hand that was actively moving in all tasks)[1]. Because UNm performance did not involve error correction, the obtained correlation values reflected the influence of reflex interactions and were regarded as baseline values (Ridderikhoff, Peper et al., 2005). Therefore, for all participants the R_{EC} values obtained for each condition in AB and KT were corrected by subtracting the corresponding mean values for UNm, as obtained for that participant. In addition, the correlation between the duration of simultaneously performed cycles (R_{CD}) was calculated as an index of the strength of interlimb interactions, with higher values of R_{CD} reflecting stronger coupling (Ridderikhoff, Peper et al., 2005). For statistical analyses, R_{EC} and R_{CD} were transformed into normally distributed values using the Fisher transform. For clarity, the untransformed values are presented in the Results.

2.4.2 Spatial Coordination. The first two cycles were removed from the analysis and additional cycles were removed if the pattern was not executed in the correct direction. The cycles included in the analysis were low-pass filtered (2nd-order directional Butterworth filter, cut-off frequency 10 Hz). The velocity profile of movements in the *Y* dimension (anterior-posterior) was used to calculate movement amplitudes. Amplitudes were calculated as $X_{amp} = |X_{t,a}—X_{t,b}|$ and $Y_{amp} = |Y_{t,c}—Y_{t,d}|$, where *t,a* and *t,b* indicate the time of peak positive and peak negative velocity, and *t,c* and *t,d* indicate the time of zero crossing in the velocity profile in positive and negative direction (Franz et al., 1991). The index of circularity was defined as X_{amp}/Y_{amp}, yielding 1 for drawing a perfect circle and 0 for drawing a perfect vertical line. For each trial, the index of circularity was averaged over the included cycles, and the corresponding standard deviation was taken as a spatial variability measure. Drawing performance was also assessed in terms of smoothness of the shapes drawn, which was operationalized as the number of velocity peaks in the tangential velocity signal per cycle that exceeded a velocity threshold of 2.0 cm/s: $|v_{max}—v_{min}| > 2.0$ cm/s. This threshold value was chosen based on the study of Volman, Wijnroks, and Vermeer (2002), taking into account the frequency of the drawing movements. For each trial, the mean number of peaks was calculated over the included cycles.

2.5 Statistical Analysis

The repeated-measures analyses of variances (ANOVAs) for the temporal tasks involved between-participants factor Age (6/7 years, 10/11 years, 14/15 years, adults) and within-participant factors Task (AB, KT, and UNm; unless specified otherwise), Pattern (IP, AP), Shift (-30°, 0°), and Direction (flexion, extension) for the temporal tasks. Direction was taken as a factor because effects have been reported to concentrate around the moment of pacing (Fink, Foo, Jirsa, & Kelso, 2000). First, Ψ and CSD_{Ψ} were examined separately for UN and UNm (with a 0°-phase shift) using ANOVAs with factor Age, and, for UNm, Pattern. Second, AE_{Φ} and CSD_{Φ} as obtained for AB, KT, and UNm (with a 0°-phase shift) were examined using an ANOVA with factors Age, Task, Pattern, and Direction. Next, strategic comparisons between two tasks were performed to uncover how the different sources of interlimb interaction contributed to coordinative stability (see Introduction). The difference between two tasks in each condition was submitted to an ANOVA with factors Age, Pattern, Direction, and, if applicable, Shift. The stabilizing effect of planning interactions was assessed by comparing CSD_{Φ} between AB and KT, and between AB and UNm (see Introduction). The stabilizing influences of error correction were assessed by comparing CSD_{Φ} between KT and UNm. Entraining effects of reflex interactions were assessed by comparing Ψ between UN and UNm. Furthermore, R_{EC} and R_{CD} were analyzed using an ANOVA with factors Age, Pattern, Direction, and Task. For R_{EC} tasks AB and KT were examined; for R_{CD} tasks AB, KT, and UNm.

For the spatial tasks, Age was included as between-participants factor and Condition (unimanual, bimanual-same, bimanual-different) as within-participant factor. The corresponding ANOVAs were conducted for line and circle drawing separately, examining the index of circularity, its variability, and the smoothness of drawing.

In all ANOVAs, Greenhouse-Geisser adjustment of degrees of freedom was applied if the assumption of sphericity was violated. Effect sizes were based on the partial eta squared (η_p^2, Cohen, 1988). Significant effects ($p < .05$) were further scrutinized using post hoc paired-samples *t* tests. All significant effects obtained in the ANOVAs are presented in Table 3. In the Results section only results involving

Table 3 Results ANOVAs

Variable	Effects	*F*-value	*p*	η_p^2	Comparison levels
CSD*$_{\Psi}$ *UN	Age	$F_{3,36} = 24.3$	.001	.53	*see text*
CSD*$_{\Psi}$ *UNm	Pattern	$F_{1,36} = 7.3$	.05	.16	IP (25.0°) < AP (31.4°)
	Age	$F_{3,36} = 7.9$	.001	.35	*see text*
***AE*$_{\Phi}$**	Direction	$F_{1,36} = 6.8$	.05	.16	flexion (24.6°) < extension (26.0°)
	Task	$F_{2,72} = 42.1$	.001	.54	AB (10.3°) < KT (34.7°) & UNm (20.1°)
	Pattern	$F_{1,36} = 9.7$	.01	.21	IP (22.7°) < AP (27.9°)
	Age	$F_{3,36} = 3.9$	.05	.25	*see text*
	Task×Direction	$F_{2,72} = 4.9$	.05	.12	AB flexion (8.26°) < extension (12.4°), KT n.s. (35.5° and 33.9°), UNm n.s. (30.0° and 31.7°)
	Task×Age	$F_{6,72} = 4.8$	.001	.28	*see text*
***CSD*$_{\Phi}$**	Direction	$F_{1,36} = 6.8$	.05	.16	flexion (20.3°) < extension (21.5°)
	Task	$F_{1.5,52.6} = 45.2$	.001	.56	AB (15.7°) < KT (18.9°) < UNm (28.1°)
	Pattern	$F_{1,36} = 11.0$	.01	.23	IP (18.9°) < AP (22.9°)
	Age	$F_{3,36} = 18.9$	.001	.61	*see text*
ΨUNm-ΨUN	Shift	$F_{1,36} = 5.9$	.05	.14	-30° (-15.2°) < 0° (-5.94°)
	Pattern	$F_{1,36} = 4.8$	.05	.12	IP (-17.6°) < AP (-3.44°)
REC	Task	$F_{1,36} = 19.5$	.001	.35	AB (-.02) > KT (-.13)
	Age	$F_{3,36} = 3.1$	.05	.21	*see text*
	Direction×Task×Pattern	$F_{1,36} = 4.1$	.05	.10	AB = KT for flexion AP (-.05 and -.03), AB > KT for flexion IP (-.07 vs. -.19), extension IP (.05 vs. -.13), and AP (-.01 vs. -.15)

RCD	Direction	$F_{1,36} = 15.1$	.001	.30	flexion (.24) > extension (.19)
	Task	$F_{2,72} = 104$	.001	.74	AB (.49) > KT (.11) & UNm (.06)
	Age	$F_{3,36} = 3.2$	.05	.21	*see text*
	Task×Direction	$F_{1.6,58.7} = 4.2$	.05	.11	AB flexion (.54) > extension (.44), KT n.s. (.13 and .09), UNm n.s. (.06 and .05)
	Task×Direction×Age	$F_{4.9,58.7} = 2.6$	.05	.18	*see text*
	Task×Pattern	$F_{2,72} = 7.9$	.001	.18	IP: AB (.53) > KT (.16) > UNm (-.02), AP: AB (.45) > KT (.06) & UNm (.13)
CI circle	Condition	$F_{2,72} = 99.5$	.001	.73	uni (0.94) & bi-same (0.94) < bi-diff (0.78)
	Condition×Age	$F_{6,72} = 2.6$	.05	.18	*see text*
CI line	Condition	$F_{1.2,41.5} = 144$	.001	.80	uni (0.04) & bi-same (0.05) < bi-diff (0.10)
	Age	$F_{3,36} = 17.8$	.001	.60	*see text*
SDCI circle	Condition	$F_{1.2,41.6} = 13.0$	.001	.27	uni (0.09) & bi-same (0.10) < bi-diff (0.13)
	Age	$F_{3,36} = 23.4$	.001	.66	*see text*
SDCI line	Condition	$F_{1.4,51.4} = 162$	.001	.82	uni (0.03) & bi-same (0.03) < bi-diff (0.07)
	Condition×Age	$F_{4.3,51.4} = 4.7$	.01	.31	*see text*
	Age	$F_{3,36} = 43.8$	.001	.79	*see text*

Abbreviations: CSD_{Ψ}: circular standard deviation of the relative phase between the hand and metronome; AE_{Φ}: absolute error of the relative phase between the hands, CSD_{Φ}: circular standard deviation of the relative phase between the hands; Ψ: relative phase between the hand and the metronome; R_{EC}: error correction correlation; R_{CD}: cycle duration correlation; *CI* = circularity index; SD_{CI} = standard deviation of the circularity index; AB = active bimanual coordination; KT = kinesthetic tracking; UNm = unimanual coordination with a metronome with a motor as distractor; UN = unimanual coordination with a metronome; IP = in-phase coordination; AP = antiphase coordination; uni = unimanual drawing; bi-same = bimanual, drawing of the same shapes; bi-diff = bimanual drawing of different shapes; n.s. = not significant.

factor Age are discussed, to focus on changes as a result of development. Values are presented as mean [between-participants *SD*].

3. Results

3.1 Temporal Coordination

Several cycles were removed from the analysis, due to incorrect task performance (see Data analysis). In particular the 6/7-year olds had difficulties to meet the task requirements regarding the coordination between the hands and synchronization with the pacing signal. Considerably more cycles were removed for this group (519) than for the older groups (on average 89.5 per group).

3.1.1 Accuracy and Variability of Unimanual and Bimanual Performance. The relative phase between the actively moving (left) hand and the metronome in tasks UN (6.71° [29.4°]) and UNm (-0.77° [35.0°]) was not affected by Age: all age groups were equally accurate in timing their movements in accordance with the metronome. Variability in the relative phase between hand and metronome, however, decreased with age in task UN (cf. Table 3). The 6/7-year olds (47.7° [11.7°]) were significantly more variable in coordinating their movements than the three older age groups while the adults (15.5° [4.10°]) were less variable than the three younger age groups (10/11: 24.5° [10.5°]; 14/15: 21.9° [7.21°]). In UNm, variability also decreased with age: the 6/7-year olds (39.6° [12.6°]) were significantly more variable than the 14/15-year olds (23.2° [6.01°]) and the adults (18.9° [3.51°]), and the 10/11-year olds (31.2° [14.7°]) were more variable than the adults as well. Unimanual coordination with the metronome was thus adequately executed in all age groups, and the variability of these movements decreased with age.

The absolute error of the relative phase between the hands (AE_{Φ}) decreased with age: the 6/7-year olds were less accurate than the 14/15-year olds and the adults, and the 10/11-year olds were less accurate than the adults (see Tables 3 and 4). In addition, differences between age groups varied over tasks: for AB the 6/7-year olds were less accurate than all older age groups and for UNm both the 6/7- and 10/11-year olds were less accurate than the 14/15-year olds and the adults. In task KT, AE_{Φ} did not differ significantly over the age groups (see Table 4).

In all three bimanual tasks variability of relative phase decreased with age: CSD_{Φ} differed significantly between all groups, except for the 10/11- and 14/15-

Table 4 Absolute Error of the Relative Phase Between the Hands

Age	AB	KT	UNm
6/7	16.8 [4.56]	30.4 [17.9]	46.4 [21.3]
10/11	8.84 [3.44]	35.5 [19.0]	39.5 [15.8]
14/15	7.59 [3.22]	36.3 [13.9]	21.6 [15.5]
Adults	8.01 [3.49]	36.5 [12.2]	15.8 [10.2]

The absolute error in the relative phase between the hands (AE_{Φ}) for the four age groups in all tasks in which two hands were involved (AB, KT, and UNm), presented as mean [between-participants *SD*] in degrees.

Table 5 Circular Standard Deviation of the Relative Phase Between the Hands

Age	AB	KT	UNm
6/7	24.1 [5.32]	28.7 [10.3]	39.4 [10.3]
10/11	16.2 [4.72]	18.9 [6.00]	31.6 [16.3]
14/15	13.0 [2.84]	16.1 [3.21]	22.7 [5.06]
Adults	9.7 [1.58]	11.8 [4.96]	18.7 [3.41]

Circular standard deviation of the relative phase between the hands (CSD_{Φ}) for the four age groups in all tasks in which two hands were involved (AB, KT, and UNm), presented as mean [between-participants *SD*] in degrees.

year olds. In addition, CSD_{Φ} varied over tasks, being smallest in AB, larger in KT, and largest in UNm (see Table 5). As this effect did not interact with Age (cf. Table 3), the enhanced stability (revealed by lower CSD_{Φ}) in task KT relative to UNm indicates that all age groups were able to intentionally use afferent information to stabilize the pattern by correcting for relative phase errors. In addition, the high stability obtained for AB performance indicates that participants in all age groups increased stability by actively planning the bimanual coordination pattern. Because overall performance improved with age, the strategic comparisons between the tasks (cf. Table 2) were conducted to examine how each of the three interlimb interactions contributed to these improvements, and whether the outcome of these comparisons differed over the four age groups. This is discussed in the next section.

3.1.2 Strategic Comparisons. *Planning*. To determine how the stability of the coordination pattern was affected by the planning process, AB and KT were compared with respect to CSD_{Φ} (cf. Table 2). Because error correction has been found to be minimally involved in task AB when planning by itself can engender sufficient coordinative stability (de Boer et al., 2011; Ridderikhoff, Peper et al., 2005), the stabilizing effect of movement planning was assessed by comparing AB to UNm as well. Values of the KT and UNm conditions (with a 0°-phase shift) were subtracted from the matched AB conditions for all participants and tested in two separate ANOVAs. The negative differences in the comparisons of AB and KT (-3.16° [7.86°]) and AB and UNm (-12.4° [13.7°]) reflected the stabilizing influence of planning interactions. The absence of a main effect of age in the two comparisons revealed that the relative contribution of planning to the stabilization of the coordination pattern did not change during development for the tested age groups (cf. Table 3).

Correction. The stabilizing effect of interactions aimed at error correction was assessed by comparing CSD_{Φ} between KT and UNm. For all participants, the values of UNm with a 0°-phase shift were subtracted from the matched KT conditions. The negative difference between KT and UNm (-9.21° [15.0°]) revealed the stabilizing effect of error correction. Similar as to planning interactions, the absence of an effect of age showed that the relative stabilizing contributions of error correction did not change during development over the ages examined (cf. Table 3).

Reflex. Reflex interactions between the limbs result in (unintentional) attraction of the phasing of the active movement toward IP or AP coordination with the passive movement. Hence, the entraining influences of the passive movements were evaluated by examining the changes in Ψ in response to the applied phase shifts. The effect of shift showed that -30° and 0° differed significantly from each other (-15.2° [36.1°] and -5.9° [35.9°], respectively), showing attraction to the passively moving limb. This effect did not differ between age groups (cf. Table 3).

3.1.3 Correlations. The error correction correlation (R_{EC}) was examined for tasks AB and KT, i.e., the two tasks in which error correction could be present (cf. Table 3). As mentioned, the values in these tasks were corrected with respect to the baseline values obtained for UNm. The effect of age showed that the 6/7-year olds exhibited less error correction (.01 [.14]) than the adults (-.11 [.09]). The degree of error correction obtained for the 10/11-year olds (-.10 [.13]) and the 14/15-year olds (-.06 [.12]) was statistically equivalent to that of the adults. Thus, although the relative stabilizing contributions of error correction did not change with age (cf., comparison CSD_{Φ} between KT and UNm), the degree of error correction increased after the age of 6/7.

Analysis of the cycle duration correlation (R_{CD}) showed that coupling strength increased with age (cf. Table 3): R_{CD} was significantly larger for the 14/15-year olds (.25 [.07]) and the adults (.26 [.05]) than the 6/7-year olds (.17 [.08]). The 10/11-year olds (.19 [.11]) did not differ from the other groups. Post hoc analyses of the interaction between task, direction, and age showed additional age differences (see Figure 1). Whereas for the younger ages only AB differed from KT and UNm (i.e., for the 6/7- and 10/11-year olds during flexion and extension, for the 14/15-year olds during extension only), all three tasks differed from each other for the older ages (i.e., for the 14/15-year olds during flexion, for the adults during flexion and extension). Thus for all ages, interlimb coupling was stronger in AB

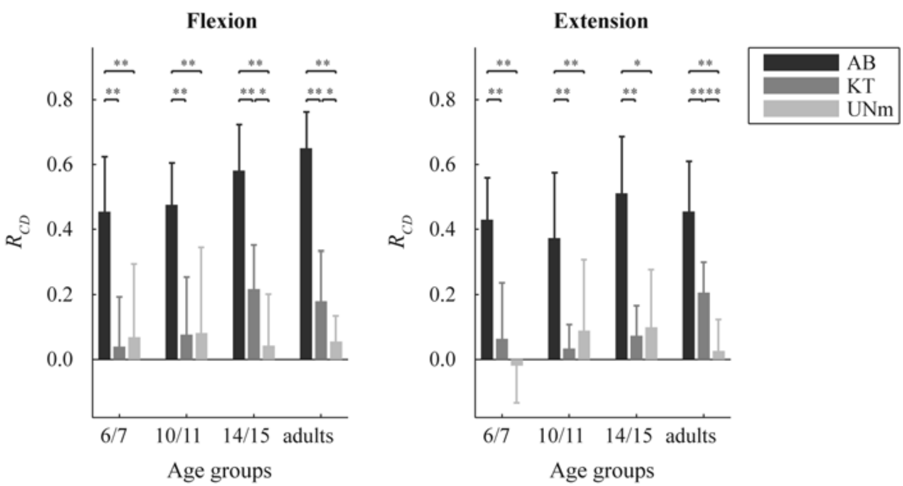

Figure 1 —Cycle duration correlation (R_{CD}) presented for the four age groups for AB, KT, and UNm, calculated separately for cycles from peak flexion to peak flexion and from peak extension to peak extension. Error bars represent between-participants *SD*. Significant differences between tasks are indicated (* $p < .05$, ** $p < .01$).

than in KT and UNm, and for the older ages this coupling was also stronger in KT than in UNm. This latter difference showed that the correction interactions (viz. comparison between KT and UNm, cf. Table 2) contributed more to interlimb coupling after the age of 10/11 (during flexion and extension) and the age of 14/15 (during extension).

3.2 Spatial Coordination: Drawing Different Shapes

3.2.1 Mean Circularity Index. With increasing age, overall performance of circle drawing did not change (cf. Table 3), whereas line drawing improved: performance of the 14/15-year olds (0.05 [0.01]) and the adults (0.05 [0.01]) was better than that of the 10/11-year olds (0.07 [0.01]), which in turn was better than performance of the 6/7-year olds (0.09 [0.03]).

Drawing two different shapes deteriorated performance of both circle and line drawing, showing that the two hands influenced each other (as reflected by the effect of condition, cf. Table 3). For line drawing this effect did not differ over the age groups: the circularity index of line drawing in unimanual drawing (0.04 [0.02]) was better than bimanual-same drawing (0.05 [0.02]) and both were superior to that in that obtained for bimanual-different drawing (0.10 [0.04]). For circle drawing an age-related difference was obtained when the two different shapes were drawn simultaneously. In all age groups bimanual-different drawing was performed worse than bimanual-same and unimanual drawing, but the size of deterioration differed between age groups: the decrease in circularity in bimanual-different drawing compared with bimanual-same drawing was larger for the 6/7-, 10/11-, and 14/15-year olds than for the adults, In addition, compared with unimanual drawing, the decrease in circularity was larger for the 14/15-year olds than for the adults (cf. Figure 2).

3.2.2 Variability of the Circularity Index. Variability in circularity of circle drawing decreased with age: the 6/7-year olds (0.17 [0.05]) were more variable in drawing circles than the older groups, and the 10/11-year olds (0.11 [0.02]) and the 14/15-year olds (0.09 [0.02]) were more variable than the adults (0.06 [0.01]). For line drawing, variability in general decreased with age (cf. Figure 3), indicating

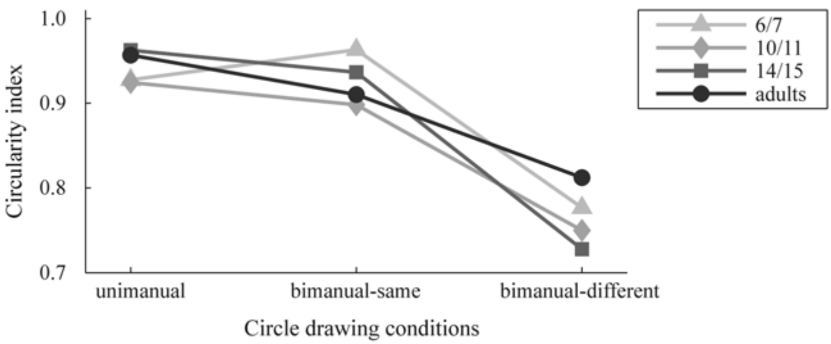

Figure 2 — Mean circularity index of circle drawing with the right hand, presented for the four age groups, for unimanual drawing, bimanual-same drawing, and bimanual-different drawing.

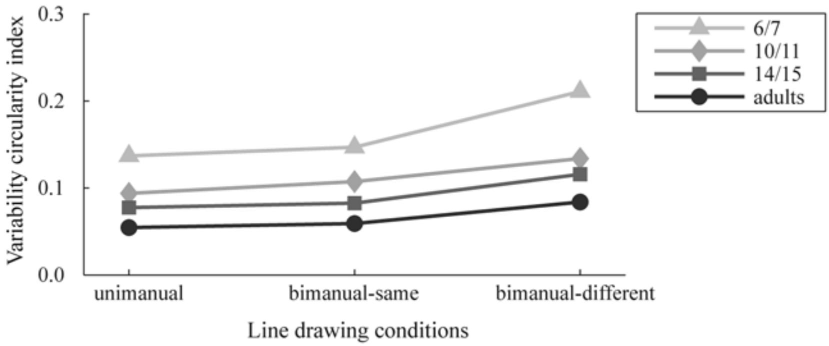

Figure 3 —Variability of circularity index of line drawing with the left hand, presented for the four age groups, for unimanual drawing, bimanual-same drawing, and bimanual-different drawing.

that drawing consistency improved gradually with age for the different conditions. For all age groups unimanual and bimanual-same drawing was less variable than bimanual-different drawing, but for the three drawing conditions the age groups differed significantly from one another (unimanual: 6/7 and 10/11 > 14/15 > adults; bimanual-same: 6/7 > 10/11 > 14/15 and adults; bimanual-different: 6/7 > 10/11 and 14/15 > adults).

3.2.3. Smoothness. The drawing movements became smoother with age (viz. the number of velocity peaks decreased with age). Both circles and lines were drawn smoother by the adults than the children, whereas the children age groups did not differ from one another (circle drawing: 6/7 year: 6.27 [0.57], 10/11 year: 6.26 [0.85], 14/15 year: 6.19 [1.25], adults: 4.59 [0.43]; line drawing: 6/7 year: 5.04 [0.55], 10/11 year: 5.16 [0.68], 14/15 year: 4.61 [0.69], adults: 4.11 [0.17]).

4. Discussion

The aim of the current study was to examine how spatial and temporal coupling of the hands change as a function of development. Temporal bimanual coupling improved with age, as evidenced by the accuracy and variability of the relative phase between the hands. Because improvements in temporal bimanual coordination as a function of development have been shown in previous studies (Fagard et al., 2001; Fitzpatrick et al., 1996; Muetzel et al., 2008; Wolff et al., 1998), we focused on unraveling these improvements in terms of three interlimb interactions governing bimanual stability: planning, correction, and reflex interactions. This is discussed in Section 4.1. Regarding the spatial task, overall drawing performance improved with age, in line with previous drawing experiments (Lantero & Ringenbach, 2007; Robertson, 2001). Because simultaneously drawing two different shapes has provided vital information regarding spatial coupling (i.e., Franz et al., 1996; Franz et al., 1991; Swinnen et al., 2001), we examined this task in the four age groups; this is discussed in Section 4.2.

Although the development of bimanual coordination may involve a multitude of changes in brain networks and functioning, we were particularly interested in the match between our results and the myelination of the CC. After all, the CC plays an essential role in interhemispheric communication, and thus is likely to contribute substantially to the interlimb interactions that we examined. The results are therefore discussed further in relation to myelination of the CC and mirror activity (see Section 4.3) and in relation to the direction of CC myelination as reported in the literature (see Section 4.4).

4.1 Temporal Coupling and Planning, Correction, and Reflex Interactions

For all age groups differences were observed between the four tasks, revealing the stabilizing contribution of the three sources of interlimb interaction to the bimanual coordination pattern. To recall, three sources of interaction between the limbs were examined, related to (1) movement planning of the bimanual coordination pattern, (2) correction of observed errors in the relative phase, and (3) reflexes inducing entrainment to the contralateral hand. These interactions were examined by pairwise comparison of two tasks that differed in one source of interaction only (cf. Introduction).

Results showed that all three sources of interaction contributed to the stability of the coordination pattern: planning and error interactions reduced the relative phase variability and reflex interactions enhanced stability by entraining the actively moving hand toward IP and AP coordination. However, the relative contributions of the three interlimb interactions did not differ over the examined age groups, suggesting that from the age of 6 to adulthood the degree to which the achieved coordinative stability depended on the three sources of interaction did not change. Already at the age of 6 stabilizing properties of all interactions contributed to the stability of IP and AP coordination.

The absence of age effects in the pairwise comparisons may have resulted from insufficient sensitivity to unravel developmental changes in these interactions. In particular, the differences in relative phase variability in task UNm across the four age groups (cf. Table 4) may have hampered these comparisons. With increasing age, participants showed significantly less variability of the relative phase between the hands in UNm, which may have resulted from overall improvement in the timing their movements as reflected by the reduced variability with age in task UN. As a result the older age groups had less opportunity (relative to younger ages) to improve stability in the tasks involving more sources of interlimb interaction (KT and AB). Hence, a potential increase in stabilizing effort due to planning and correction interactions at older ages may have been masked.

Despite the absence of age-related effects in the abovementioned comparisons, results regarding cycle duration correlation (R_{CD}) showed that interlimb coupling strength increased with age. Furthermore, both R_{CD} and the error correction correlation (R_{EC}) indicated that error correction improved significantly over the examined ages. The amount of error correction was significantly smaller for the 6/7-year olds than for adults. In addition, analysis of R_{CD} indicated that error correction interactions also improved after the age of 10/11 and 14/15, resulting in stronger coupling for the older groups when performing task KT (involving error correction) than when performing task UNm (not involving error correction).

Taken together, these results indicate that over the age span of 6 years to young adulthood, coordinative stability improved with age. However, the degree to which the achieved stability resulted from planning and reflex interactions did not change significantly with age. That is, although performance was less stable in the younger children, the degree to which this stability depended on entrainment to the contralateral hand and on active planning of the bimanual coordination pattern was comparable to that in the older children and adults. In contrast, although its effect was not visible at the level of relative phase variability, the use of kinesthetic feedback to correct errors in relative phasing improved significantly from the age of 6 to young adulthood.

4.2 Spatial Coupling in Bimanual Line-Circle Drawing

With increasing age, participants drew more consistently (i.e., less variably) and smoother (i.e., with less velocity changes). Overall circularity of circle drawing did not improve with age, whereas it did for line drawing. These results correspond to bimanual drawing performance observed in previous experiments with children aged 4–8 years and adults (Lantero & Ringenbach, 2007; Ringenbach & Amazeen, 2005).

Spatial coupling between the hands was assessed by comparing performance in the bimanual-different condition to the unimanual and bimanual-same conditions. Drawing the circle and line together resulted in attraction of both hands to each other (i.e., resulting in vertically-oriented oval-shaped circles and lines), yielding deteriorated performance relative to unimanual and bimanual-same drawing (Franz et al., 1996; Franz et al., 1991; Volman, 2005). In all age groups performance decreased when drawing the line and circle simultaneously. The decrease in circularity of circles was smaller for adults than for children, revealing that adults were better in executing two different spatial tasks with both hands. For line drawing the effect of bimanual-different drawing did not differ over the age groups.

In sum, previously observed age-related improvements in unimanual and bimanual circle drawing were also observed in the present experiment. Furthermore, spatial coupling between the hands was stronger for children aged 6–15 than for adults. No difference was observed between the children groups. This suggests that after the age of 15, the spatial coupling between the hands decreased such that adults are better in executing different movements with the two hands simultaneously.

4.3 Myelination of the Corpus Callosum and Temporal Coupling

With respect to the temporal coupling tasks, improvements across the age span of 6–15 year were expected to be more pronounced for AP than IP coordination as a result of enhanced interhemispheric inhibition of mirror activity due to increased myelination of the CC (Cincotta & Ziemann, 2008; Cohen et al., 1967; Hubers et al., 2008). However, the results did not reveal any differences in developmental improvement rates of the two coordination patterns. In all age groups IP was performed more accurately and less variably than AP, and the increases in stability and accuracy across development occurred in parallel for IP and AP coordination.

Although this parallel development of IP and AP coordination from the age of 6 to young adulthood was not expected, it was in line with the results of at least two previous studies (Fagard & Pezé, 1997; Wolff et al., 1998), whereas another experiment did reveal larger developmental effects for the AP pattern (Marion, Kilian, Naramor, & Brown, 2003). Unfortunately, however, most studies examined only one bimanual coordination pattern, and thus did not provide information in this regard (Lantero & Ringenbach, 2007; Muetzel et al., 2008; Pellegrini, Andrade, & Teixeira, 2004; Robertson, 2001).

The current results suggest that the stability difference between IP and AP coordination is present at young ages and improvements of these two coordination patterns develop in parallel. Therefore, although myelination of CC has been shown to enhance bimanual coordination (Muetzel et al., 2008), these improvements appear not to result from enhanced inhibition of mirror activity. After all, improved suppression of the mirror symmetric coupling between the limbs would only benefit AP coordination. This topic may be further scrutinized by examining younger children and by increasing movement frequency, since IP-AP stability differences are more pronounced at higher frequencies (Haken et al., 1985; Schöner et al., 1986). Moreover, it would be useful to assess mirror activity (during unimanual performance) as well, using fine-grained analysis of EMG activity (cf. Ridderikhoff, Daffertshofer, Peper, & Beek, 2005). The current results, however, suggest that, for the examined age span, the observed general improvements in bimanual coordination stem primarily from other developmental changes.

4.4 Direction of Myelination and Spatial and Temporal Coupling

Previous studies examining CC myelination using magnetic resonance imaging have suggested that the CC myelinates across childhood in an anterior-posterior direction, with largest myelination rates of the anterior CC between the ages of 3–6 and largest myelination rates of the posterior CC between the ages of 6 to 15 (Giedd et al., 1996; Thompson et al., 2000). Since callosotomy studies showed predominant involvement of the anterior CC in temporal coupling and the posterior CC in spatial coupling (Eliassen et al., 1999; Ouimet et al., 2010), temporal coupling may be expected to change more in early development, whereas developmental changes in spatial coupling would be more prominent at later ages.

The present study revealed that development across the examined ages resulted in less spatial interference between the two hands after the age of 14/15. Adults differed from children, but no differences were observed between the children age groups, whereas spatial performance measures not directly related to spatial coupling (viz., smoothness and variability of circularity) improved significantly over all age groups. This corresponds to the general expectation that improvement in spatial coupling (viz. decreased interference) would manifest itself relatively late in development. Temporal coupling on the other hand (indexed by relative phase accuracy and variability) changed over all age groups, indicating that these improvements indeed set in at younger ages.

Although our behavioral data showed a general correspondence to the previously reported direction of myelination of CC, they did not exactly fit the identified moments of peak myelination rates. As such, CC myelination appears not to be related to changes in spatial and temporal coordination in a 1:1 fashion. Developmental improvements in temporal and spatial coordination appear to become manifest somewhat after the moment of peak myelination rate of the corresponding CC parts, suggesting that increased myelination of CC fibers may be a prerequisite for further developmental improvement. Furthermore, although largest myelination rates were found between 3–6 years in anterior CC fibers and between 6 to15 years in posterior fibers, myelination of these fibers continues at lower rates until the early twenties (Giedd et al., 1996; Thompson et al., 2000). Therefore, it remains to be established whether the observed improvements in temporal and spatial coordination are dependent on these ongoing myelination processes, or whether they are primarily due to the development of specific control processes following peak myelination rates.

Although myelination of the CC plays a significant role in the development of bimanual temporal and spatial coordination, this does not exclude the importance of other brain areas and connections: bimanual movements are not controlled by one specific area in the brain, but rather by a distributed network of different brain sites (Debaere et al., 2001; Swinnen, 2002). Thus, even if myelination results in enhanced temporal and spatial coupling between the hands, this does not rule out the contributions of other brain areas and connections. On the contrary, it is highly plausible that increased temporal and spatial coordination is engendered by changes in pertinent neural networks.

4.5 Concluding Remarks

Based on the results in the present experiment, three conclusions can be drawn. First, for the temporal task, coordinative stability improved with age. Although stability increased over the age groups, the achieved stability resulted from similar relative contributions of planning and reflex interactions in all age groups. Correction interactions on the contrary improved with age, showing enhanced use of kinesthetic feedback. Second, at our low movement frequency we did not find indications of differential improvements as a function of age for the IP and AP coordination patterns. Hence, although myelination of the CC contributes to improved bimanual coordination (Muetzel et al., 2008), the current results did not provide evidence that this was due to enhanced inhibition of mirror activity. Third, the results correspond to the suggested anterior-posterior direction of CC myelination with temporal coupling improving at relatively young ages and spatial coupling improving more markedly at older ages. However, although CC myelination probably plays a significant role in the development of bimanual temporal and spatial coupling, presumably various other areas are involved as well (Debaere et al., 2001; Swinnen, 2002).

Note

1. Ridderikhoff et al. (2007) showed that whereas the correlation between the signed error and the next full cycle is influenced by between- and within-hand correlations, the correlation between the signed error and the next half cycle is not. Furthermore, analysis showed that errors in the current experiment were mainly corrected during the first half cycle and hardly in the subsequent half cycles.

References

Carson, R.G., Goodman, D., Kelso, J.A.S., & Elliott, D. (1995). Phase transitions and critical fluctuations in rhythmic coordination of ipsilateral hand and foot. *Journal of Motor Behavior, 27,* 211–224. PubMed doi:10.1080/00222895.1995.9941711

Cincotta, M., & Ziemann, U. (2008). Neurophysiology of unimanual motor control and mirror movements. *Clinical Neurophysiology, 119,* 744–762. PubMed doi:10.1016/j.clinph.2007.11.047

Cohen, H.J., Taft, L.T., Mahadeviah, M.S., & Birch, H.G. (1967). Developmental changes in overflow in normal and aberrantly functioning children. *The Journal of Pediatrics, 71,* 39–47. PubMed doi:10.1016/S0022-3476(67)80228-2

Cohen, J. (1988). *Statistical power analysis for the behavioral sciences* (2nd ed.). Hillsdale, NJ: Lawrence Erlbaum Associates.

Daffertshofer, A., Peper, C.E., & Beek, P.J. (2005). Stabilization of bimanual coordination due to active interhemispheric inhibition: A dynamical account. *Biological Cybernetics, 92,* 101–109. PubMed doi:10.1007/s00422-004-0539-6

de Boer, B.J., Peper, C.E., & Beek, P.J. (2011). Frequency-induced changes in interlimb interactions: increasing manifestations of closed-loop control. *Behavioural Brain Research, 220,* 202–214. PubMed doi:10.1016/j.bbr.2011.01.057

Debaere, F., Swinnen, S.P., Beatse, E., Sunaert, S., Van Hecke, P., & Duysens, J. (2001). Brain areas involved in interlimb coordination: A distributed network. *NeuroImage, 14,* 947–958. PubMed doi:10.1006/nimg.2001.0892

Deoni, S.C., Mercure, E., Blasi, A., Gasston, D., Thomson, A., Johnson, M., et al. (2011). Mapping infant brain myelination with magnetic resonance imaging. *The Journal of Neuroscience, 31,* 784–791. PubMed doi:10.1523/JNEUROSCI.2106-10.2011

Eliassen, J.C., Baynes, K., & Gazzaniga, M.S. (1999). Direction information coordinated via the posterior third of the corpus callosum during bimanual movements. *Experimental Brain Research, 128,* 573–577. PubMed doi:10.1007/s002210050884

Eliassen, J.C., Baynes, K., & Gazzaniga, M.S. (2000). Anterior and posterior callosal contributions to simultaneous bimanual movements of the hands and fingers. *Brain, 123,* 2501–2511. PubMed doi:10.1093/brain/123.12.2501

Fagard, J., Hardy-Leger, I., Kervella, C., & Marks, A. (2001). Changes in interhemispheric transfer rate and the development of bimanual coordination during childhood. *Journal of Experimental Child Psychology, 80,* 1–22. PubMed doi:10.1006/jecp.2000.2623

Fagard, J., Morioka, M., & Wolff, P.H. (1985). Early stages in the acquisition of a bimanual motor skill. *Neuropsychologia, 23,* 535–543. PubMed doi:10.1016/0028-3932(85)90007-7

Fagard, J., & Pezé, A. (1997). Age changes in interlimb coupling and the development of bimanual coordination. *Journal of Motor Behavior, 29,* 199–208. PubMed doi:10.1080/00222899709600835

Fink, P.W., Foo, P., Jirsa, V.K., & Kelso, J.A.S. (2000). Local and global stabilization of coordination by sensory information. *Experimental Brain Research, 134,* 9–20. PubMed doi:10.1007/s002210000439

Fitzpatrick, P., Schmidt, R.C., & Lockman, J.L. (1996). Dynamical patterns in the development of clapping. *Child Development, 67,* 2691–2708. doi:10.2307/1131747

Franz, E.A. (1997). Spatial coupling in the coordination of complex actions. *The Quarterly Journal of Experimental Psychology, 50,* 684–704. PubMed doi: dx.doi.org/10.1080/713755726

Franz, E.A., Eliassen, J.C., Ivry, R.B., & Gazzaniga, M.S. (1996). Dissociation of spatial and temporal coupling in the bimanual movements of callosotomy patients. *Psychological Science, 7,* 306–310. doi:10.1111/j.1467-9280.1996.tb00379.x

Franz, E.A., Zelaznik, H.N., & McCabe, G. (1991). Spatial topological constraints in a bimanual task. *Acta Psychologica, 77,* 137–151. PubMed doi:10.1016/0001-6918(91)90028-X

Giedd, J.N., Lalonde, F.M., Celano, M.J., White, S.L., Wallace, G.L., Lee, N.R., et al. (2009). Anatomical brain magnetic resonance imaging of typically developing children and adolescents. *Journal of the American Academy of Child and Adolescent Psychiatry, 48,* 465–470. PubMed doi:10.1097/CHI.0b013e31819f2715

Giedd, J.N., Rumsey, J.M., Castellanos, F.X., Rajapakse, J.C., Kaysen, D., Vaituzis, A.C., et al. (1996). A quantitative MRI study of the corpus callosum in children and adolescents. *Brain Research. Developmental Brain Research, 91,* 274–280. PubMed doi:10.1016/0165-3806(95)00193-X

Haken, H., Kelso, J.A.S., & Bunz, H. (1985). A theoretical model of phase transitions in human hand movements. *Biological Cybernetics, 51,* 347–356. PubMed doi:10.1007/BF00336922

Hübers, A., Orekhov, Y., & Ziemann, U. (2008). Interhemispheric motor inhibition: Its role in controlling electromyographic mirror activity. *The European Journal of Neuroscience, 28,* 364–371. PubMed doi:10.1111/j.1460-9568.2008.06335.x

Ivry, R.B., & Hazeltine, E. (1999). Subcortical locus of temporal coupling in the bimanual movements of a callosotomy patient. *Human Movement Science, 18,* 345–375. doi:10.1016/S0167-9457(99)00014-7

Kelso, J.A.S. (1984). Phase transitions and critical behavior in human bimanual coordination. *The American Journal of Physiology, 246,* R1000–R1004. PubMed

Kennerley, S.W., Diedrichsen, J., Hazeltine, E., Semjen, A., & Ivry, R.B. (2002). Callosotomy patients exhibit temporal uncoupling during continuous bimanual movements. *Nature Neuroscience, 5,* 376–381. PubMed doi:10.1038/nn822

Lantero, D.A., & Ringenbach, S.D. (2007). Developmental differences in the use of visual information during a continuous bimanual coordination task. *Journal of Motor Behavior, 39,* 139–155. PubMed doi:10.3200/JMBR.39.2.139-157

Mardia, K.V. (1972). *Statistical analysis of directional data*. London: Academic Press.

Marion, S.D., Kilian, S.C., Naramor, T.L., & Brown, W.S. (2003). Normal development of bimanual coordination: Visuomotor and interhemispheric contributions. *Developmental Neuropsychology, 23,* 399–421. PubMed doi:10.1207/S15326942DN2303_6

Mayston, M.J., Harrison, L.M., & Stephens, J.A. (1999). A neurophysiological study of mirror movements in adults and children. *Annals of Neurology, 45,* 583–594. PubMed doi:10.1002/1531-8249(199905)45:5<583::AID-ANA6>3.0.CO;2-W

Muetzel, R. L., Collins, P. F., Mueller, B. A., Schissel, A. M., Lim, K. O., & Luciana, M. (2008). The development of corpus callosum microstructure and associations with bimanual task performance in healthy adolescents. *NeuroImage, 39,* 1918–1925. PubMed doi:10.1016/j.neuroimage.2007.10.018

Oldfield, R.C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9,* 97–113. PubMed doi:10.1016/0028-3932(71)90067-4

Ouimet, C., Jolicoeur, P., Lassonde, M., Ptito, A., Paggi, A., Foschi, N., et al. (2010). Bimanual crossed-uncrossed difference and asynchrony of normal, anterior- and totally-split-brain individuals. *Neuropsychologia, 48,* 3802–3814. PubMed doi:10.1016/j.neuropsychologia.2010.09.003

Pellegrini, A.M., Andrade, E.C., & Teixeira, L.A. (2004). Attending to the non-preferred hand improves bimanual coordination in children. *Human Movement Science, 23,* 447–460. PubMed doi:10.1016/j.humov.2004.08.017

Rajapakse, J.C., Giedd, J.N., Rumsey, J.M., Vaituzis, A.C., Hamburger, S.D., & Rapoport, J.L. (1996). Regional MRI measurements of the corpus callosum: A methodological and developmental study. *Brain & Development, 18,* 379–388. PubMed doi:10.1016/0387-7604(96)00034-4

Ridderikhoff, A., Daffertshofer, A., Peper, C.E., & Beek, P.J. (2005). Mirrored EMG activity during unimanual rhythmic movements. *Neuroscience Letters, 381,* 228–233. PubMed doi:10.1016/j.neulet.2005.02.041

Ridderikhoff, A., Peper, C.E., & Beek, P.J. (2005). Unraveling interlimb interactions underlying bimanual coordination. *Journal of Neurophysiology, 94,* 3112–3125. PubMed doi:10.1152/jn.01077.2004

Ridderikhoff, A., Peper, C.E., & Beek, P.J. (2006). Bilateral phase entrainment by movement-elicited afference contributes equally to the stability of in-phase and antiphase coordination. *Neuroscience Letters, 399,* 71–75. PubMed doi:10.1016/j.neulet.2006.01.026

Ridderikhoff, A., Peper, C.E., & Beek, P.J. (2007). Error correction in bimanual coordination benefits from bilateral muscle activity: Evidence from kinesthetic tracking. *Experimental Brain Research, 181,* 31–48. PubMed doi:10.1007/s00221-007-0902-7

Ridderikhoff, A., Peper, C.E., & Beek, P.J. (2008). Attentional loads associated with interlimb interactions underlying rhythmic bimanual coordination. *Cognition, 109,* 372–388. PubMed doi:10.1016/j.cognition.2008.10.002

Ringenbach, S.D., & Amazeen, P.G. (2005). How do children control rate, amplitude, and coordination stability during bimanual circle drawing? *Ecological Psychology, 17,* 1–18. doi:10.1207/s15326969eco1701_1

Robertson, S.D. (2001). Development of bimanual skill: The search for stable patterns of coordination. *Journal of Motor Behavior, 33,* 114–126. PubMed doi:10.1080/00222890109603144

Schöner, G., Haken, H., & Kelso, J.A.S. (1986). A stochastic theory of phase transitions in human hand movement. *Biological Cybernetics, 53,* 247–257. PubMed doi:10.1007/BF00336995

Serrien, D.J., Li, Y., Steyvers, M., Debaere, F., & Swinnen, S.P. (2001). Proprioceptive regulation of interlimb behavior: Interference between passive movement and active coordination dynamics. *Experimental Brain Research, 140,* 411–419. PubMed doi:10.1007/s002210100820

Swinnen, S.P. (2002). Intermanual coordination: From behavioural principles to neural-network interactions. *Nature Reviews. Neuroscience, 3,* 348–359. PubMed doi:10.1038/nrn807

Swinnen, S.P., Dounskaia, N., Levin, O., & Duysens, J. (2001). Constraints during bimanual coordination: The role of direction in relation to amplitude and force requirements. *Behavioural Brain Research, 123,* 201–218. PubMed doi:10.1016/S0166-4328(01)00210-8

Thompson, P.M., Giedd, J.N., Woods, R.P., MacDonald, D., Evans, A.C., & Toga, A.W. (2000). Growth patterns in the developing brain detected by using continuum mechanical tensor maps. *Nature, 404,* 190–193. PubMed doi:10.1038/35004593

Tuller, B., & Kelso, J.A. (1989). Environmentally-specified patterns of movement coordination in normal and split-brain subjects. *Experimental Brain Research, 75,* 306–316. PubMed doi:10.1007/BF00247936

Volman, M.J. (2005). Spatial coupling in children with hemiplegic cerebral palsy during bimanual circle and line drawing. *Motor Control, 9,* 395–416. PubMed

Volman, M.J., Wijnroks, A., & Vermeer, A. (2002). Bimanual circle drawing in children with spastic hemiparesis: Effect of coupling modes on the performance of the impaired and unimpaired arms. *Acta Psychologica, 110,* 339–356. PubMed doi:10.1016/S0001-6918(02)00041-0

Wolff, P.H., Kotwica, K., & Obregon, M. (1998). The development of interlimb coordination during bimanual finger tapping. *The International Journal of Neuroscience, 93,* 7–27. PubMed doi:10.3109/00207459808986408

Zanone, P.G., & Kelso, J.A.S. (1992). Evolution of behavioral attractors with learning: non-equilibrium phase transitions. *Journal of Experimental Psychology: Human Perception and Performance, 18,* 403–421. PubMed doi:10.1037/0096-1523.18.2.403